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Morphological Variation in the Radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) from Atlantic and Pacific Populations

by

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Abstract. *Placida dendritica* is a cosmopolitan, ascoglossan (=sacoglossan) species for which geographic variants have been difficult to define. However, examination of 54 radulae, 34 of these with an SEM, revealed a geographic pattern of Pacific Basin teeth with a cutting edge of regular truncate denticles, while North Atlantic and Mediterranean specimens had an edge of irregular, conical denticles. Body lengths ranged from 2 to 20 mm, ascending tooth row from 6 to 18 teeth, descending tooth row from 18 to 78, and total number of teeth for individuals from 28 to 93. Loose teeth in the ascus were recorded only in Australian and New Zealand samples. Highest tooth counts were from British Columbian specimens of 7 and 8 mm body length, and the next highest counts from 3 and 4 mm Australian and New Zealand specimens. Eleven contrasting collection sites are described, and the algal genus *Derbesia* is added to *P. dendritica* prey items.

INTRODUCTION

One of the consequences of geographic isolation, and a basic tenent in biology, is that genetic variants can more readily become established and thereby greatly hasten speciation. Over great distances, one easily assumes that there has been some degree of anatomical diversity and may even feel obligated to find it. Thus, it is not surprising that whenever a sea slug resembling the European sea slug *Placida* (*Hermaea*) *dendritica* (Alder & Hancock, 1843) was reported from a distant geographic region it was assumed to be a new species and confidently designated as such. At that time, the full spectrum of variation that can be encompassed by seasonal and individual variations was not appreciated. Thus, this animal has been known as *P. aoteana* Powell, 1937, in New Zealand, *P. babai* Marcus, 1982, in Japan, and *P. ornata* MacFarland, 1966, in California. The current taxonomic consensus (Thompson, 1973, 1976; Gascoigne, 1976; Jensen, 1983; Marcus *in* Baba, 1986) is that a single species (*Placida dendritica*) ranges from Norway to the Mediterranean Sea; from Newfoundland to the Florida Keys and to Curaçao in the Lesser Antilles; from British Columbia to Mexico; and from Japan to eastern Australia and New Zealand.

That there are no reported differences in general anatomy nor in radular morphology between populations of this worldwide species is truly remarkable. Available literature implies that even its algal prey is consistent worldwide, the siphonalean Chlorophyta genus *Codium*. Clark & Franz (1969) went so far as to state that it was highly unlikely that *Placida dendritica* could have existed in New England prior to a recent establishment of *Codium fragile* (Suringar) Hariot in that area. Recent examination of material in my collections, however, indicates that (1) *P. dendritica* does occur in areas devoid of *Codium*, and that (2) radular morphology does differ regionally.

MATERIALS AND METHODS

Specimens collected personally in New Zealand, Australia, Japan, British Columbia, Nova Scotia, and Newfoundland were also photographed alive with color transparencies. Additional preserved material was kindly supplied by the individuals indicated in Table 1, which lists localities, col-

Table 1

List of localities, collectors, dates, total numbers of specimens, and number of *Placida dendritica* radula examined by SEM.

Locality	Collector	Date	Total specimens	SEM
N.Z., Leigh	J. S. Bleakney	April 1981	54	2
N.Z., Otago Bay	J. S. Bleakney	11 May 1981	7	1
Aust., Botany Bay	J. S. Bleakney	17 Jan. 1981	42	4
Japan, Seto	J. S. Bleakney	1 Nov. 1980	3	1
Japan, Osaka Bay	I. Hamatani	18 Feb. 1961	6	3
B.C., Vancouver Isl.	J. S. Bleakney	Aug. 1980	4	1
B.C., Triangle Isl.	P. Lambert	21 Aug. 1974	2	2
B.C., Vancouver Isl.	G. Gibson	21 May 1988	18	3
N.S., Chester Basin	J. S. Bleakney	31 Aug. 1969	1	1
N.S., Bear River	J. S. Bleakney	26 July 1970	3	2
Newfd., Logy Bay	J. S. Bleakney	7 Aug. 1970	1	1
Ireland, Co. Donegal	B. E. Picton	29 May 1988	3	2
England, Loo	A. Kress	March 1970	20	4
Spain	J. Ortea	?	4	4
Italy, Naples	Panceri	1866	4	3
			172	34

lectors, dates, number of specimens available for this study, and the number of radulae examined by SEM.

Radulae from each locality were prepared for SEM examination by the tissue solubilizer method of BLEAKNEY (1982) and 148 SEMs taken. The tiny penial style proved difficult to prepare for SEM, but several samples proved adequate for verification of structures suspected from light microscopy observation. Standard microscope slide mounts of radulae and penial styles were photographed, and additionally many of the radulae were photographed through a microscope during and/or at the end of the tissue solubilizer treatment. Overall, 130 black and white photographs were taken.

RESULTS AND DISCUSSION

Diversity of Algal Food

The morphology of *Placida dendritica* teeth can be altered by feeding on algae. The tooth tip can be blunted and the cutting edge worn down (Figure 20) and in some cases even chipped and broken (Figures 1, 2, 5).

Although *Codium* is the reported main food of *Placida dendritica* (JENSEN, 1980), *Bryopsis* was mentioned by MILLEN (1980) for British Columbia and by THOMPSON (1976) for Europe. However, in Newfoundland and Nova Scotia where *Codium* is absent and *Bryopsis* is very rare, I found this ascoglossan feeding and spawning upon *Derbesia marina* (Lymgbye) Sal. This genus is also a member of the Siphonales, an algal group with coenocytic filaments much preferred by algal sapsuckers. This small alga is easily overlooked, as it usually occurs as a small tuft, mat, or coating on the surface of larger algae or upon animal exoskeletons. Interestingly, specimens of *P. dendritica* collected at Seto, Japan, were on *Derbesia lamourouxii* (J. Agardh) Solier (=*marina*?) in a region where this ascoglossan has been reported to feed only upon *Codium* (BABA, 1955, 1986). At the Leigh Marine Laboratory, New Zealand, *P. aoteana* was collected from both *Codium adhaerens*

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Explanation of Figures 1 to 7

Figure 1. Portion of radular ribbon with attached teeth from 20-mm long *Placida dendritica,* Osaka, Japan. Note three worn teeth at left in descending tooth row, and broken tip of the functional first tooth at upper right. (SEM, ×450; scale bar = 100 μm.)

Figure 2. Detail of wear in tooth no. 3 in Figure 1. (SEM, ×4500; bar = 10 m.)

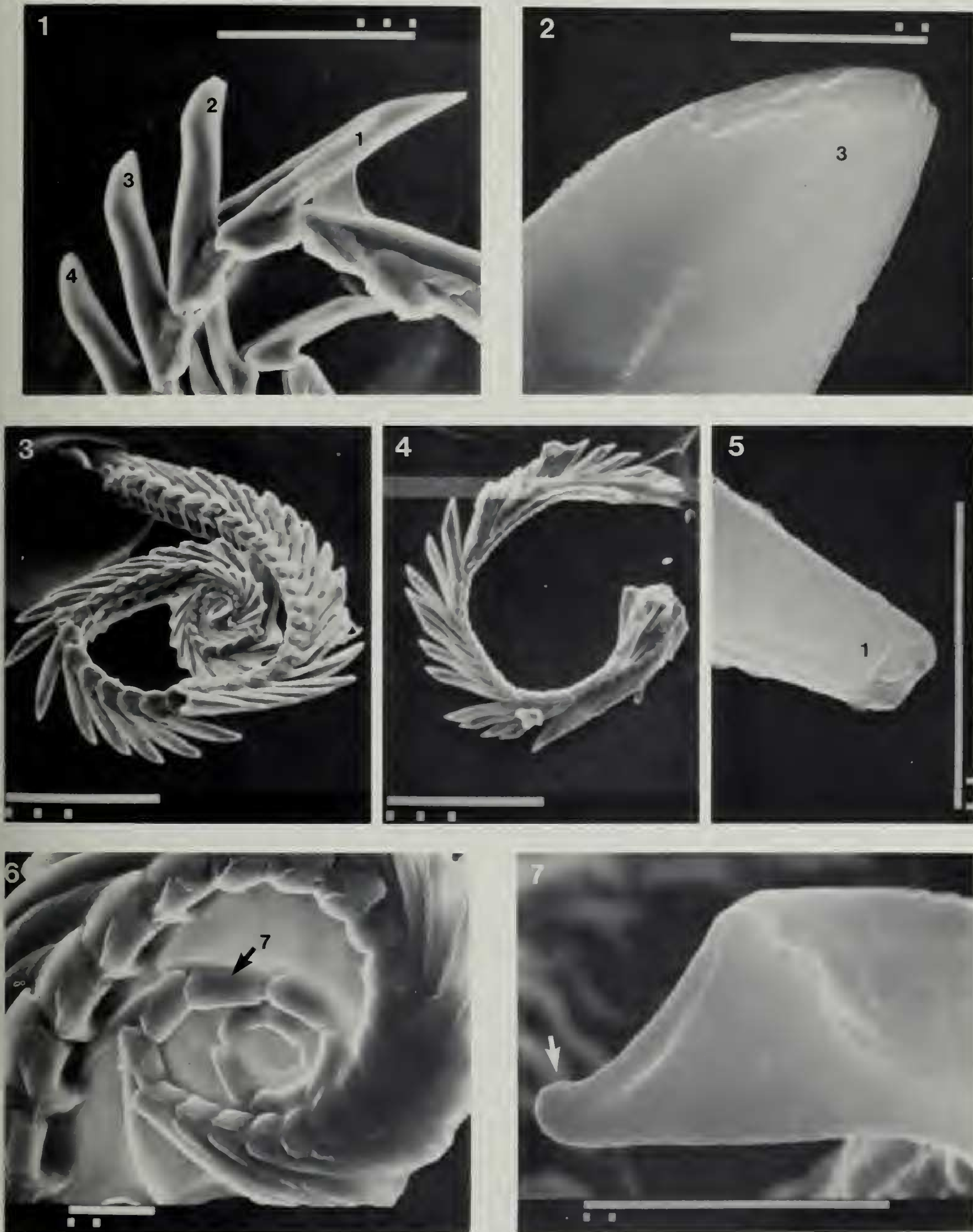
Figure 3. Typical long, coiled radula from 8-mm long British Columbia specimen. (SEM, ×300; bar = 100 μm.)

Figure 4. Terminal ascus with jumble of loose teeth (not coiled) noted only in a few specimens from Australia and New Zealand. From a 3-mm long specimen from Sydney, Australia. (SEM, ×300; bar = 100 μm.)

Figure 5. Detail of broken tip of tooth no. 1 in Figure 1. (SEM, ×7000; bar = 10 μm.)

Figure 6. Detail of series of seven juvenile teeth in coil of radula from 6-mm specimen, Triangle Island, British Columbia. (SEM, ×2000; bar = 10 μm.)

Figure 7. Tip of hollow penial style from 5-mm specimen from Leigh, New Zealand, showing thickened, turned up tip (arrow), typical of all *Placida dendritica* examined from Pacific and Atlantic regions. (SEM, ×7000; bar = 10 μm.)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2
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and *Derbesia novaezelandiae* Chapman. Slugs feeding on *Derbesia* were a paler green than those from the *Codium* plants.

It is evident that *Placida dendritica* has a somewhat wider spectrum of algal prey genera than previously assumed. Its occurrence in New England and Atlantic Canada undoubtedly preceded, and was not predicated upon, the recent establishment of *Codium* in southern New England as postulated by CLARK & FRANZ (1969).

Diversity of Habitats

CLARK & DEFREESE (1987) have recently emphasized that ascoglossans, as a group, are broadly distributed in latitude and habitat, seemingly unfettered by their trophic specialization. Remarkably, the same can be said of several species within that group, and *Placida dendritica* is a superb example. Perusal of available literature, however, does not reveal the truly astounding diversity of habitats from which this species can be collected. One simply learns that *P. dendritica* occurs on *Codium* and *Bryopsis* subtidally, without any mention of substrate, tidal and temperature extremes, winter ice conditions, or general description of local environs.

That malacologists may have a better understanding of the adaptive capabilities of *Placida dendritica,* and be encouraged to seek it out, the following 11 examples (from personal experience, unless otherwise noted) have been selected. To what degree these extremely different environments modify this species' growth and reproductive patterns at the geographic or regional level is unknown.

(1) Newfoundland, Avalon Peninsula, Logy Bay Marine Laboratory. Rocky coast of sheer cliffs, tidal range 0.9 to 1.9 m, too exposed and stormy for safe anchorage of research vessels, temperatures from −1.5 to 14°C with drift ice and icebergs in winter. *Placida dendritica* was found on tufts of *Derbesia marina* on valves of *Mytilus* sp. attached to rocks at a depth of 8 m.

(2) Nova Scotia, Annapolis Basin, Bear River estuary. Broad, shallow, muddy, tidal river, commercial clam digging, twice-daily tides of 7.8 to 10.2 m, ice blocks in winter. *Placida dendritica* was found in a mixed collection of algae and hydroids scraped from the surface of wood-encased, bridge piers exposed at E.L.W.S. tide.

(3) Nova Scotia, Chester Basin, Atlantic coast. Tides 1.5 to 2.2 m, seasonal temperature range of −1 to 16°C, in winter sea ice often freezes shore to shore for months. *Placida dendritica* was found on *Derbesia marina* on valves of *Modiolus modiolus* Linn. attached to rocks at a depth of 4 m.

(4) Connecticut, Noank, Mystic River estuary (CLARK, 1975). *Zostera marina* Linn. dominant in bay area, *Placida dendritica* found on *Codium fragile* attached to small rocks on sand/mud bottom, attached to wooden bridge trestle, and to wooden hull of grounded ship, at depths of 0.5 m to 3 m.

(5) Florida Keys (CLARK, 1975:43, no further information).

(6) Lesser Antilles, Curaçao, Piscadera Baai (MARCUS & MARCUS, 1970)—"From algae and *Thalassia* in outer bay."

(7) British Columbia, outer coast of Vancouver Island, Bamfield Marine Laboratory. Strong currents, rocky coast with many islands, nutrient rich waters, diverse and abundant marine flora and fauna, tidal range 2.7 to 3.9 m, and seasonal range of sea temperatures near 7 to 14°C. *Placida dendritica* was found on *Codium fragile* growing on rock faces at depths of 2 to 6 m.

(8) Japan, Honshu Island, Seto Marine Laboratory. Area of intensive tourism, fishing, agriculture, marine transport facilities, highly polluted, sea temperatures from 12 to 28°C under influence of warm Kuroshio Current, many tropical and sub-tropical species, tides to 1.8 m. *Placida dendritica* was found on tufts of *Derbesia lamourouxii* (=*marina*?) growing on the surface of tunicates attached to rocks on a bottom of sand, rock, cobble, and mud at a depth of 5 m.

(9) Australia, Sydney, south shore bays of Botany Bay. Area of immense coastal sand dunes, bay shallow, warm, with commercial oyster racks, tides from 1.2 to 1.8 m, at E.L.W. with 0.1 to 0.3 m water depth over a ripple sand substrate; shallows have *Zostera* beds while *Posidonia australis* Hook. f. grass dominates in deeper water. *Placida dendritica* was found on *Codium fragile* attached to cockles (*Cardium rackette*) buried in the sand.

(10) New Zealand, North Island, Leigh Marine Laboratory. Shore of jagged platforms of conglomerate and mudstone, with abundant pools, caves and crevices, tidal range of 2.6 to 3.5 m, sea temperature from 14 to 21°C. *Placida dendritica* was found subtidally on rock-encrusting mats of *Codium adhaerens,* and in the tide pools on *Derbesia novaezelandiae* epiphytic on the brown alga *Carpophyllum plumosum.*

(11) New Zealand, South Island, Dunedin, Portobello Marine Laboratory in Otago Harbour. A 20-km long sheltered inlet, laboratory is 8 km from entrance at the tip of peninsula jutting into the harbor, a restriction generating tidal currents of 3 to 4 knots which keep this section clear of harbor silts, harbor surface temperatures from 5 to 19°C, shore of basalt cliffs and ledges with rock fragments at cliff bases in shallow water. *Placida dendritica* found on *Bryopsis plumosa* (but not on equally abundant *Codium fragile*) attached to rocks in 0.5 m of water at E.L.W.

These 11 examples cover an impressive spectrum of habitats, but it is equally evident that several of the algal species fed upon by ascoglossans have similar, nearly global distributions. This may be relevant to the general question of why there is not more speciation within certain genera of ascoglossans. Perhaps the global constancy of this ascoglossan species is a reflection of the seemingly immutable persistence of its host plants.

Number of Teeth

Within a range of body lengths of 2 to 20 mm, the number of teeth in the ascending row varied from 6 to 18,

Table 2

Numbers of radular teeth in *Placida dendritica* relative to body length, from 10 geographic regions. NZ = New Zealand; Au = Australia; Jp = Japan; BC = British Columbia; NS = Nova Scotia; Nf = Newfoundland; Ir = Ireland; En = England; Sp = Spain; It = Italy. Figures in parentheses are conservative tooth counts, as those specimens had a compact jumble of free teeth in their ascus.

Body length (mm)	Ascending tooth row										Descending tooth row										Total number teeth									
	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It	NZ	Au	Jp	BC	NS	Nf	Ir	En	Sp	It
20	8		7								38		33								46		40							
18	8										27										35									
16										7										27										34
14	10		9								29		27								39		36							
12	8		7								34		25								42		32							
12			7										29										36							
11										8										27										35
10			6										24										30							
9							8			7							37			24							45			31
8				18										54										72						
7				15			9	9						78			50	19						93			59	28		
7				15				10						40				25						55				35		
7								8										21										29		
7								8										22										30		
7								8										22										30		
7								10										19										29		
6	10			13				10			28			48				21			38			61				31		
6				15										37										52						
5	13		7	13		10					30		24	33		20					43		31	46		30				
5				10										29										39						
4	13	12			10						30	(42+)			24						43	(35+)			34					
4	13	13									31	(22+)									44	(54+)								
4	15										(38+)										(50+)									
4	10										(38+)										(48+)									
4	11										25										36									
3		13						11				24						18				37						29		
3		14										21										35								
3		12										28										40								
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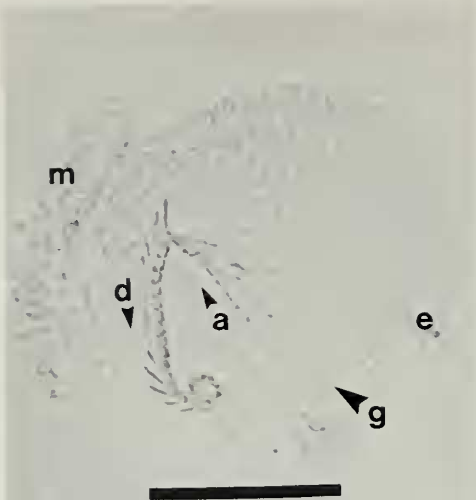
2									8										22										30	
2									8										23										31	
2									10										33										43	

Specimen totals: 11 NZ, 13 Au, 6 Jp, 4 BC, 2 NS, 1 Nf, 2 Ir, 8 En, 4 Sp, 3 It = 54 total.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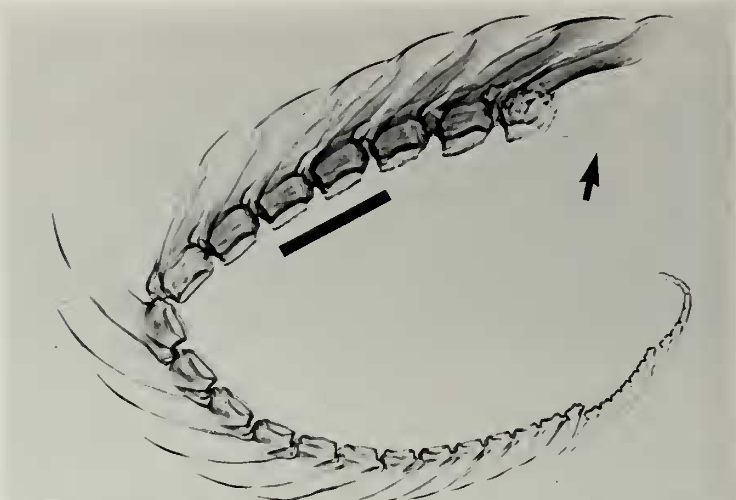

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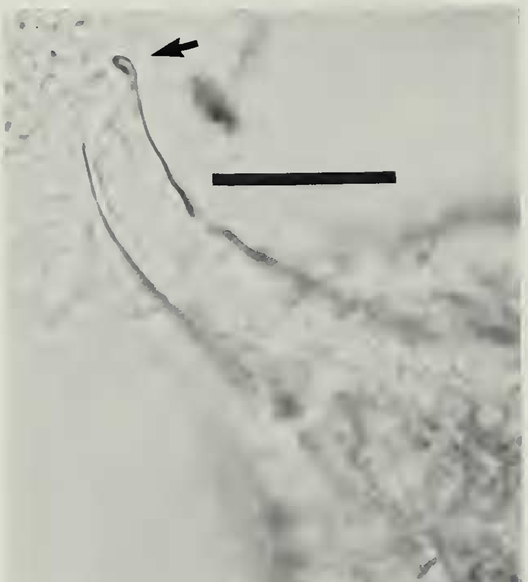

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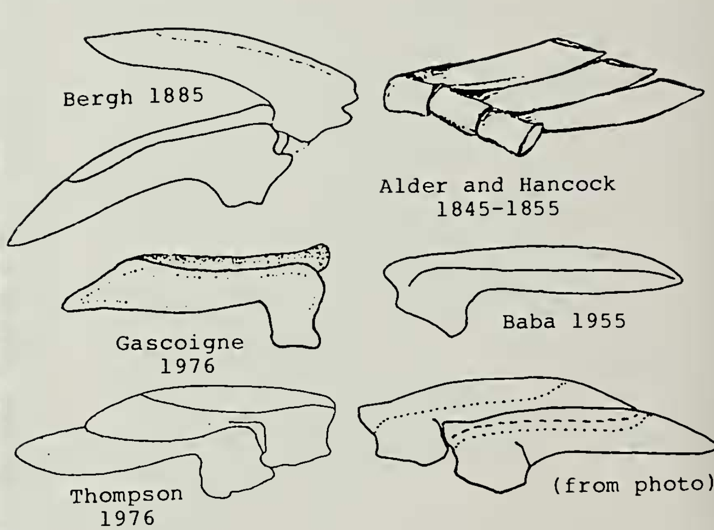
Bergh 1885
Alder and Hancock
1845-1855
Gascoigne
1976
Baba 1955
Thompson
1976
(from photo)

13

in the descending row (including ascus) from 18 to 78, and total individual counts from 28 to 93 teeth. The latter two counts were both from 7-mm long specimens. There was a thoroughly perplexing absence of positive correlation between body length and number of teeth, for most of the higher and all of the highest tooth counts are from specimens 8 mm or less in length. The greatest discrepancy within one sample was between the larger and smaller New Zealand specimens (Table 2). However, all the larger animals came from Otago, South Island, whereas the smaller ones were collected at Leigh on North Island. Is this north-south difference (particularly the low number of teeth in the ascending row of the large individuals) true for other populations on the two islands, or was this a temporal phenomenon similar to the fluctuating tooth counts reported for *Elysia chlorotica* (RAYMOND & BLEAKNEY, 1987)?

Other interesting geographic variations noted were (1) the occasional occurrence of a jumble of loose teeth in the ascus, instead of a neat coil, noted only in Australia and New Zealand (6 of 24 specimens examined) and (2) the highest tooth counts and the largest terminal radular coils limited to British Columbia.

Radular Morphology

Figure 8 is a photomicrograph of an entire buccal mass showing ascending (dorsal) tooth row, and descending (ventral) tooth row in which the teeth progressively decrease in size. The production of new teeth is evident in Figure 9 in the ascending tooth row where two insubstantial "ghost teeth" commence the series. Two such translucent teeth was the norm for most specimens of *Placida dendritica,* and these were included when counting teeth.

The descending radular limb is long, and usually continuous, terminating in a series of 5 to 7 juvenile teeth (GASCOIGNE & SARTORY, 1974) which lack fully formed, pointed, cusps on their blocklike bases (Figures 6, 9). This terminal region (in all of the geographic regions sampled) may have the configuration of a long curve (Figure 9), or be sharply hooked (Figure 8), or tightly coiled (Figures 3, 6). The classic ascoglossan sac, in which all discarded teeth are deposited forming a jumbled mass, was observed only in Australian and New Zealand specimens, where 25% of those examined (6 of 24) had an ascus sac with a jumble of teeth (Figure 4). The only potential example of loose teeth in an ascus from another geographic area, Europe, seems to be BERGH (1885:pl. V, fig. 6). However, I believe his diagram depicts a typical coil, because there are seven block-shaped teeth prior to the first strongly cusped tooth. Those extremely small, cusped teeth he included in the ascus must have been an optical artifact because *Placida dendritica* does not produce teeth that small with distinct bases and cusps. Bergh's other diagram of a radula of this species (pl. II, fig. 2) is of the typical hook-shaped, descending limb.

The morphology of individual teeth varies from straight to slightly down-curved, and the tips may be rounded, pointed, or angular. However, to determine these shapes is difficult and requires care, because a slight shift of the viewing angle (whether light microscopic or SEM) generates new proportions. An additional pitfall is that unless the teeth being examined are of the ascending row, and thus not yet used in feeding, the effect of attrition so often evident on teeth in the descending limb can create misleading outlines. Subtle differences in proportions can be detected by comparing Figures 10 and 11, where tips of the unused ascending teeth are pointed and fit closely into the pocket of each succeeding tooth, but are worn and rounded and slightly shorter in the descending tooth row (Figure 11).

Of the seven authors who have published diagrams of individual teeth, by far the best representation is that of BERGH (1885). His diagram and those of other selected authors are assembled in Figure 13, as well as a new diagram based on the present study. The two most confusing aspects of those previous diagrams are a conse-

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Explanation of Figures 8 to 13

Figure 8. Entire buccal mass from *Placida dendritica,* Chester Basin, Nova Scotia, photographed after 15 min in tissue solubilizer. Note mouth (m), esophagus (e), ascending tooth row (a) originating at large generative sac (g), and descending tooth row (d) with terminal coil of juvenile teeth. (Scale bar = 200 μm.)

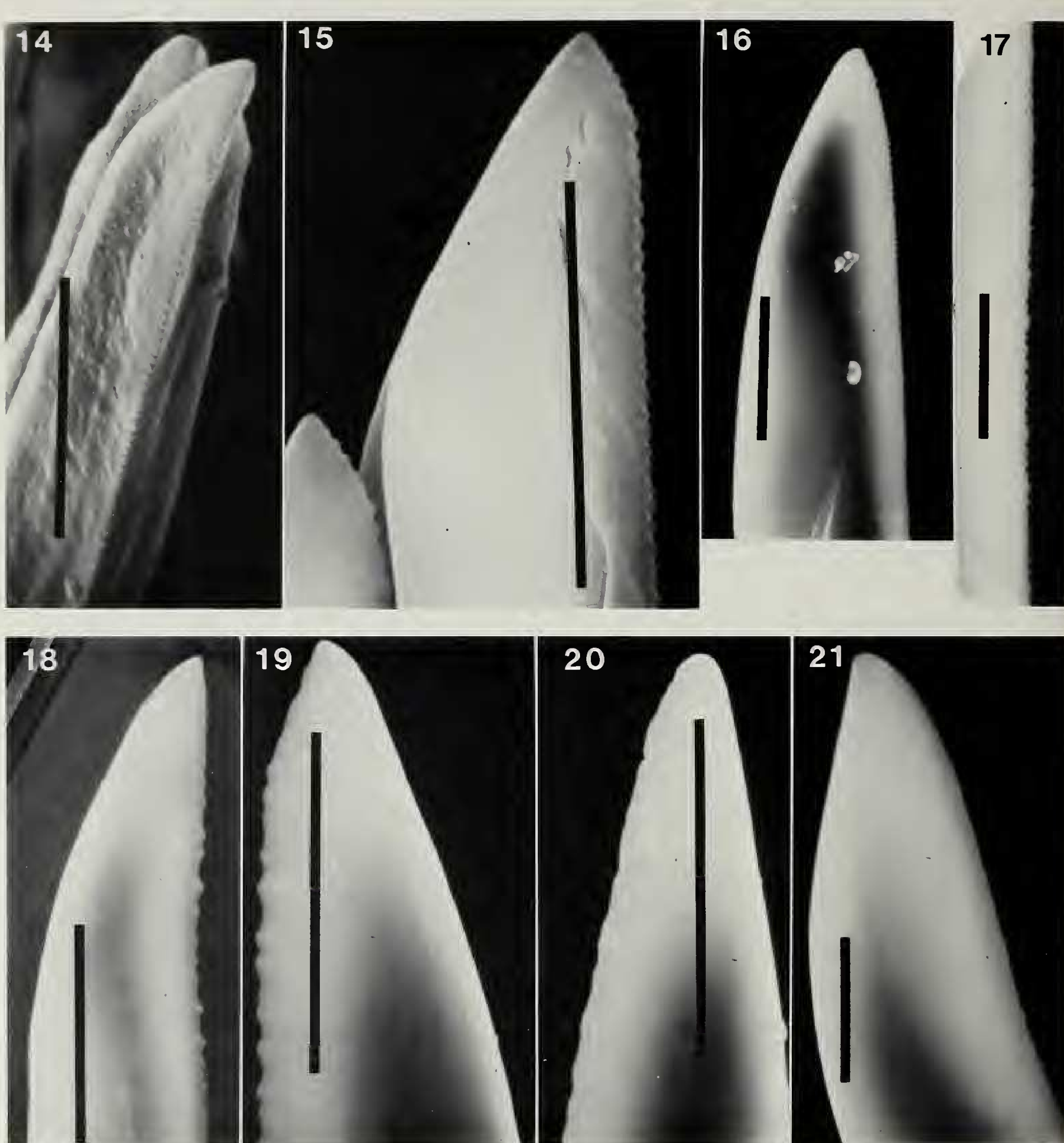
Figure 9. Radula and remnants of buccal mass of an 1866 Naples, Italy, specimen, after overnight in tissue solubilizer at 35°C. In the ascending tooth row, top of photo, are six fully formed teeth, one nearly differentiated, and ghostly outlines of two others. These "ghost teeth" (arrow) were included in the totals of numbers of teeth in the ascending rows listed in Table 2. (Scale bar = 60 μm.)

Figure 10. New, unused teeth in the ascending tooth row of an Osaka, Japan, specimen showing pointed tips closely fitted (arrow) into dorsal groove of adjacent tooth. (Scale bar = 81 μm.)

Figure 11. Three worn and broken teeth within the descending tooth row of the same radula as Figure 10.

Figure 12. Top of hollow penial style embedded in apex of penis (p) showing thickened, hooked lip (arrow) not previously reported but common to all specimens of *Placida dendritica* examined. Specimen from Otago Bay, New Zealand. (Scale bar = 20 μm.)

Figure 13. Five examples of the diversity of published illustrations of tooth morphology for *Placida dendritica,* with a sixth diagram traced from a photomicrograph of the ascending tooth row of a 9-mm specimen from Ireland. In that diagram (a lateral view) the dotted lines represent the depth of the dorsal trough and the dash line represents the serrated keel edge of the upper tooth fitted into the trough.



Explanation of Figures 14 to 21

Figures 14 to 17 are representative of radulae from the Pacific Ocean region, whereas Figures 18 to 21 are typical of specimens from the North Atlantic Ocean and Mediterranean Sea.

Figure 14. Ventral aspect of serrated edge on keel of radular tooth of 4-mm *Placida dendritica,* Sydney, Australia. (SEM, ×4500; scale bar = 10 μm.)

Figure 15. Lateral aspect of serrated edge of tooth from 4-mm long specimen, Sydney, Australia. (SEM, ×7000; bar = 10 μm.)

Figure 16. Lateral aspect of tooth from 6-mm specimen, Triangle Island, British Columbia. (SEM, ×3000; bar = 10 μm.)

Figure 17. Keel edge of 21-mm long specimen, Otago Bay, New Zealand. (SEM, ×3000; bar = 10 μm.)

Figure 18. Serrated edge of unused tooth from ascending row of 8-mm long *Placida dendritica,* Loo, England. (SEM, ×4500; bar = 10 μm.)

quence of (1) representing the bottom of the deep trough in a tooth (lateral view) as a solid line and thus implying a surface feature, rather than as a dotted line indicating a visible, subsurface feature, or (2) unnecessarily indicating the transition from lateral wall to medial keel (Figure 14) by a full-length line.

A significant tooth feature, not reported previously, is the serrated cutting edge common to all populations examined. BABA (1955) and JENSEN (1980) reported the teeth of *Placida dendritica* to be smooth edged. THOMPSON (1988) noted a "roughened" cutting edge "but not regularly denticulate" on two Mediterranean specimens from Yugoslavia. The serrations revealed by my SEM examinations are of two types, and one was limited to the Pacific Ocean samples and the other to the Atlantic Ocean and Mediterranean Sea. The serrations of all Pacific region samples are of a rather uniform series of adjacent projections, square to rectangular in outline, with a truncate to rounded free edge (Figures 14–17). The Atlantic and Mediterranean specimens have irregularly spaced, larger, sharply pointed serrations, somewhat conical with the base of the cone extending as a ridge a short distance up the side of the tooth keel (Figures 18–21).

In absolute terms, this difference in serrated edging is rather miniscule, but it is interesting that specimens from the Pacific Ocean rim differ as a group from samples from North Atlantic and Mediterranean shores. Assuming this indicates that Atlantic and Pacific populations of *Placida dendritica* have long been isolated, then one can pose pertinent zoogeographic questions about southern Africa and the Caribbean Sea. Although climatically disjunct today, there are coastal areas in southern Africa where 17 to 20% of the opisthobranch species also occur in the northern Atlantic and where less than 2% are Indo-Pacific (GOSLINER, 1987). Gosliner calculated that of the probable sister species of endemic opisthobranchs in southern Africa, 43% are known from the northern Atlantic. *Placida dendritica* has not yet been reported from southern Africa but, if it is, the tooth serrations should have the same configuration as European populations, assuming the conclusions drawn from data in the present paper are valid. The Caribbean Sea is also of special zoogeographic interest, for examination of a series of specimens of *P. dendritica* from several areas in that region could answer the intriguing question of whether those populations have an original North Atlantic or a more recent Pacific Ocean affinity.

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Figure 19. Serrated edge of tooth from another Loo specimen. (SEM, ×7000; bar = 10 μm.)

Figure 20. Worn serrated edge of a used tooth from descending tooth row of same radula as Figure 19. (SEM, ×7000; bar = 10 μm.)

Figure 21. Tooth extracted from 9-mm specimen, after 122 yr in preservation, collected near Naples, Italy, in 1866. (SEM, ×3000; bar = 10 μm.)

Penial Style Morphology

Examination of the minute, hollow, penial style under the light microscope and with SEM revealed a terminal, thickened, slightly upturned projection (Figures 7, 12), not depicted previously in diagrams by GASCOIGNE (1974) for a British sample nor by THOMPSON (1973) for an Australian specimen.

Gut Tract Branching Pattern

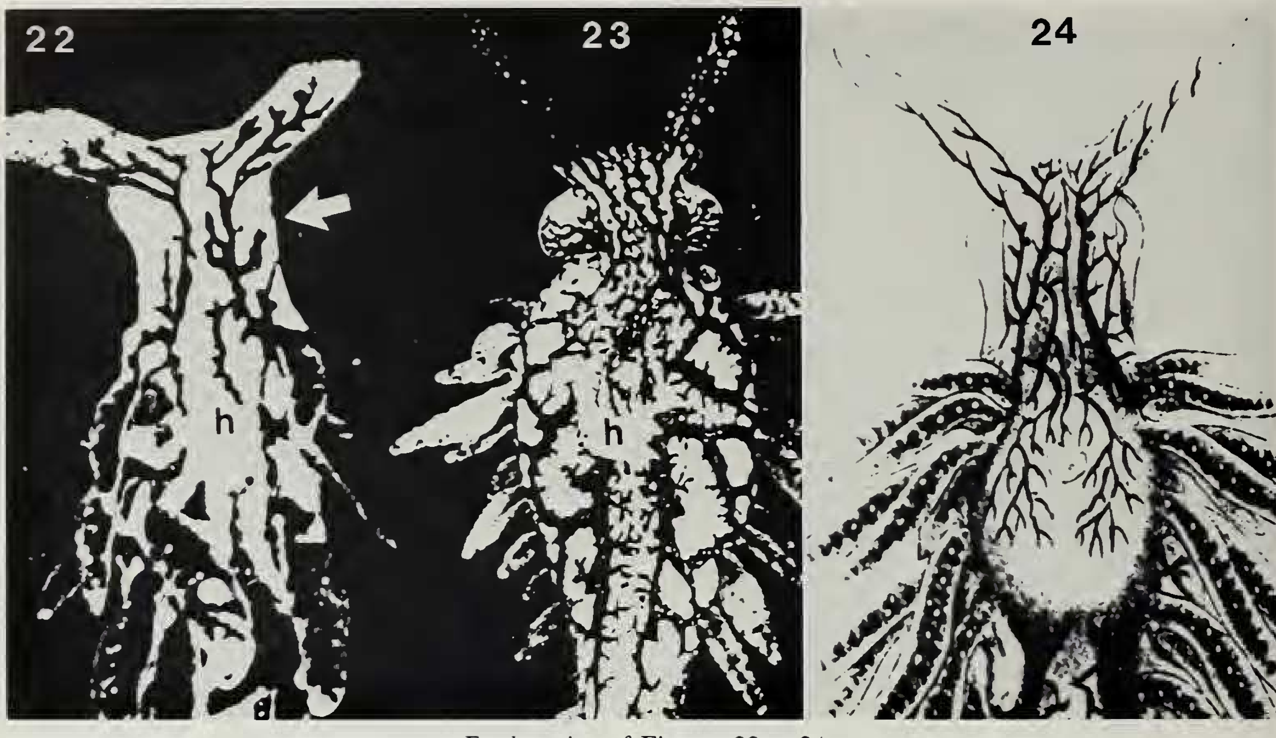
From my collection of color transparencies of live *Placida dendritica,* and one donated by A. Kress, a set of enlarged color prints were produced and comparisons made of the branching pattern of the green gut tract of specimens from New Zealand, Australia, Japan, British Columbia, Nova Scotia, Newfoundland, and England. No appreciable differences were detected. Even the basic asymmetry of branching in the heart-head region was identical. In this body region, there are major medial branches to the heart and head, and one lateral branch to the gonopore area, all originating from the right gut tract. This pattern is obvious in small specimens of 2 to 5 mm body length (Figure 22) and can readily be deciphered in larger individuals in spite of subsequent gut branch multiplication and anastomosing (Figure 23).

Most diagrams of the gut tract of *Placida dendritica* in the literature seem based upon ALDER & HANCOCK (1845–1855:fam. 3, pl. 40) which upon close examination reveals an invented bilateral symmetry as well as bifurcating, sharply pointed, terminal branches imposed upon the original print sheet by the color illustrator's delicate brush strokes (Figure 24). The real asymmetry is evident in published color photos of a British specimen (THOMPSON, 1976) and one from California (BEHRENS, 1980). Rather interestingly, MACFARLAND (1966) described this asymmetry in detail in his text (p. 40) but obscured it in his pl. 4, fig. 3 by illustrating the specimen from the left lateral aspect.

SUMMARY

Placida dendritica is a cosmopolitan, conservative ascoglossan species with reportedly identical features in Atlantic and Pacific Oceans and in Northern and Southern Hemispheres. However, examination of radulae from 10 geographic areas revealed two types of serrated edge on the teeth: one type was limited to the Pacific Ocean Basin and the other to the Mediterranean Sea and North Atlantic.

Within a range of body lengths of 2 to 20 mm, the number of teeth in the ascending row varied from 6 to 18, in the descending row (including ascus) from 18 to 78, and total individual counts from 28 to 93 teeth. There is a thoroughly perplexing absence of positive correlation between body length and number of teeth, for most of the higher and all of the highest tooth counts are from specimens 8 mm or less in size.



Explanation of Figures 22 to 24

Figure 22. Branching gut tract of 5-mm *Placida dendritica,* Logy Bay, Newfoundland. Arrow points to pair of tiny eyes. Posterior to the right eye are three major branches springing from the large right anterior gut tract: one medial branch pointing forward to the head; another medial, posterior to the first, and directed towards and onto the heart (h); and a large lateral, nearer the eye, directed towards the gonopore area (same arrow).

Figure 23. Gut tract of 7-mm specimen, Seto, Japan, demonstrating degree of expansion of branching pattern in larger specimens, but with the basic asymmetry of Figure 22 still evident.

Figure 24. Enlargement of color plate from ALDER & HANCOCK (1845–1855) revealing illustrator's invented elements of bilateral gut tract symmetry and his neat but imagined bifurcating pattern and finely tapered terminal branches.

An additional algal genus, *Derbesia,* has been added to the two previously reported algal genera (*Codium* and *Bryopsis*) upon which *Placida dendritica* is known to feed and spawn.

Descriptions of 11 contrasting collection sites indicate the broad spectrum of habitats in which this single ascoglossan species can be found.

Penial style morphology showed no geographic variation, but not previously reported is a small terminal projection.

The branching pattern of the gut tract appeared very conservative, even to the asymmetrical origin of three distinct branches from the right anterior tract that terminate on the head, heart, and gonopore areas respectively. This asymmetry was not evident in drawings from the literature, but was evident in published color photographs.

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